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# DARWIN AS A NATURALIST: DARWIN'S WORK ON CROSS POLLINATION IN PLANTS

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CHARLES DARWIN is rated as a great man, and there are really not many to-day who would dispute his title to this verdict; but he did not come easily to it.

In botany, he never did a thesis on morphology or cytology, or photosynthesis; he was puzzled rather than deranged by nomenclature; the reason that he provided for the compilation of an index to the names and authorities of all known flowering plants and their countries, in a way, is a confession that he was not a taxonomist; and a really fair all-round doctor's examination, with botany as a major, would have been likely to give him more than the proverbial trouble. He does not seem to have considered himself a botanist, and perhaps has never been admitted to the fraternity formally—though he has opened our eyes to some of the most interesting aspects of plant physiology, baring their secrets in a masterly way with the rough-and-ready direct methods and apparatus of an adept.

His earlier publications were on geology and zoology. My impression is that botanists—aside from the very few who know—looked on him in his lifetime rather as a zoologist. And yet even to-day amusement may be derived from reading what has been made public of the debate before the French Academy, when his name was under discussion for membership in the zoological section of that great body and one of the immortals was ready to place a hundred zoologists before him because of their contributions of demonstrable facts to the science.

The greatness of the man itself long stood in the way of its recognition. He had not classed himself with sufficient minuteness in the subdivision of science. Looking back on his career, it is not difficult to see that the geological problems opened up to him by the voyage of the "Beagle" would have afforded an interesting field for detailed life work in geology which would have placed him quickly among the foremost geologists of his day if he had devoted himself to them and continued to publish on that subject and for those specialists. Even the French savants saw in his barnacle studies the work of far more than a tyro; but he did not choose to devote himself to the morphology and classification of animals. So little had he been thought of generally as knowing anything of botany, that the *Gardeners' Chronicle* reviewer of his orchid book expressed himself as doubly constrained to care in critically analyzing it. He was somewhat like a versatile witness questioned individually by the members of a polyglot jury, each using and understanding his own language and getting nothing more than a minute fragment of the whole testimony: he can hardly be said to have had a hearing before his peers—of whom it would have been hard, even, to draw a full panel at any time in the world's history.

Darwin was really a philosopher. His son speaks of him as seeming to be so charged with a theorizing power that no fact, however small, could avoid releasing a stream of theory which itself magnified the fact in importance; but just enough to his theories not to condemn them unheard, so that he was willing to test what would seem to most people not at all worth testing. This is at once the key note to his life work and his greatness in influencing human thought. Though his philosophy has received unusual, and perhaps undue, attention, through clashing with some of what had become incorporated in the theology of his day, his service in molding our way of seeing nature may be coordinated with that of the great men who have reduced the movements of the planets to a physical basis and the transmutations of matter to terms of chemistry.

Curiously, the human mind of the twentieth century does not seem to be superior as a reasoning machine to that of the time of the Greeks, and it is not surprising that the general conclusions of Darwin's philosophy had been reached in one form or another all the way along the past three thousand years. That his name goes into history as their father, results from the way in which he arrived at and substantiated them rather than from their novelty: his greatness in great thought is the natural achievement of a large mind reaching its ends by way of the painstaking study of little things.

So full a discussion of Darwin from many points of view is provided in the symposium of our fellow society, the American Association for the Advancement of Science, and in the allotment of subjects for our own Darwin-session, that I should use time to little advantage if I were to go into illustration of this, outside the special field assigned me on the program—to the discussion of which I have been asked to preface this general introduction.

I wish that I might quote Darwin's first utterance on the subject that has been assigned specially to me for this meeting, but I do not know where to find it. In his autobiography, he states that in 1838 or 1839 he had begun to attend to the cross fertilization of flowers by means of insects, from having come to the conclusion in his speculations on the origin of species, that crossing played an important part in keeping specific forms constant. Even then he had noticed the floral dimorphism of *Linum*. In the preface to his book on the fertilization of orchids he explains that its publication resulted from the criticized exclusion (because of lack of space) of detailed facts substantiating an opinion expressed in his work on the origin of species, that it is apparently a universal law of nature that no hermaphrodite fertilizes itself for a perpetuity of generations—a law which he has stated in a variety of other phrases, and the suggestion of which he owed to Knight. The introductory chapter of his book on the effects of cross and self-fertilization in the vegetable kingdom indicates that this conclusion, based on his personal observations on plants, was guided to a certain extent by the experience of breeders of animals (which is detailed at length in his book on the variation of animals and plants under domestication).

It was, therefore, not a novice who entered the botanical field when, in October, 1857, Darwin contributed a one-column note to the *Gardiners' Chronicle* on bees and fertilization of kidney beans, which he was attracted to through "believing that the brush on the pistil, its backward and forward curling movement, its protrusion on the left side, and the constant alighting of the bees on the same side, were not accidental coincidences, but were connected with, perhaps necessary to, the fertilisation of the flower." His subsequent papers and books, vivifying floral ecology, were therefore as inevitable from one who was moved by a new teleology in natural science as was the superb publication of a half century earlier by Sprengel, who, seeing the petal-hairs of a Geranium, sought after their meaning in the firm conviction that the wise Author of nature had not created even a hair in vain.

Darwin's publications in this field are not numerous; omitting abstracts and reprints of papers published in full, and later editions and translations, they number only twenty-two.[1] They are remarkably direct in purpose, simple in treatment, clear in reasoning, and free from a controversial or dictatorial spirit. His own observations and experiments were rarely accepted at their face value, but were checked up with rather unusual care; and, as we now know from his published letters, his conclusions were commonly subjected to the criticism of a very select private audience before going to the world at large.

The comprehensiveness of the studies underlying these publications may be indicated by the statement that

[1] See bibliography at end.

nearly 350 genera of plants, represented by about 600 species (several of them in a number of contrasted forms and varieties), are made the subject of comment. No insignificant proportion of this large number were under observation or experimental cultivation through a considerable number of years—the series on which the "Cross and Self-Fertilization" volume was based having been grown in numbers and with painstaking care through more than a decade; and the plants measured and the seeds counted were very many. No observer was so insignificant that his observations escaped analysis if they came to the knowledge of the great naturalist, though Darwin was sorely tried by the positive statement of some non-existent facts; and some of the prettiest workings of his mind are shown in the elimination of untenable conclusions which had been drawn by predecessors whose observations were recorded in sufficient detail to permit another to winnow them afresh. Enthusiasm in fitting his own observations into his theories occasionally led to error when facts were scanty or incompletely made out, but in such cases these were usually employed with a word of caution and errors were eliminated with a charming candor when discovered subsequently; and few writers have more gracefully accepted rectifications by others—even when bluntly phrased or embodied in aggressive criticism, as was sometimes the case.

First, last and always, his studies were directed to the species question, but in his pollination studies, as in every other field that he entered, he bent himself to collateral details with the zeal of a specialist. He was never oblivious to the treacherous frailty of small numbers and few series; but his innate soundness of judgment was checked and confirmed, here and there, through the rehandling of his data by one to whom the analysis of figures was a specialty. The dainty instruments of precision in the use of which physiologists train their undergraduate students, were neither used nor desired by him;

but his experiments were devised with very unusual expertness and, like his figures, made to reveal their own defects and reenforce one another as indicating directions of high probability even where they were seen to stop far short of proof.

The problems which Darwin here set before himself for solution were primarily the explanation of natural phenomena—most of which others had observed in a general way—which in his belief could not be meaningless. Though doubtless not his first essay, his first publication on the subject, in 1857, primarily stated observed facts in *Phaseolus* and attacked them in this spirit, but incidentally he analyzed the reasons why and how bees visit flowers and what their intelligence is, and faced the broad question why varieties of beans do not freely mix if their flowers are really so formed as to secure frequent intercrossing. The behavior of introduced plants separated from their natural pollinators, further came into the next paper, with a distinct enunciation of Knight's law. Why Vincas do not seed; what their pollinators are; the details and meaning of what Dr. Gray has called heterogony, understanding which gave him unparalleled satisfaction; why flowers of two or even three nominal genera should sometimes appear on one plant of *Catasetum;* the substantiation of Knight's law by detailed arguments of adaptation selected from a single family of plants; the reason why *Lythrum salicaria* is represented by three sets of individuals as distinct from each other in floral characters as if they belonged to different species, and incidentally why *Lagerstrœmia* should possess a (less clearly analyzed) stamen-variability; why the wild oxlip should be held for a hybrid between other closely related primroses and why these are specifically distinct; an extensive experimental testing of the utility underlying Knight's law; and a comparative analysis of heterogony, sex-separation, and cleistogamy: these were the questions set for answer in subsequent publications.

The methods by which the problems were attacked were neither many nor complicated. Patience and forethought and perseverance are their chief characteristics. Observation, not exclusive of any discernible fact; experimentation, with control of the incidental results of manipulation; testing the parent condition of seeds supposed to be pure; consideration of alternative explanations of phenomena, and especially of those opposed to the conclusions adopted; counting, weighing, measuring —almost beyond belief; ingenious substitutions for insects in laboratory and garden observations on structures concerned in pollination; watching insects at work on flowers and supplementing such observation by notation of the record of their visits afforded by the flowers themselves; confirming the identity of doubtful pollinia on a moth by restoring their original color through moistening them; field observations at all hours and under all climatic conditions; ascertaining pollen-tube development in prepotency questions; painstaking pollinations to cover numerous permutations: such were the methods.

The results of Darwin's work in this field are not easily epitomized. It is not going too far to say that he secured universal recognition of Sprengel's unheeded demonstration that the structure of many flowers serves to ensure their pollination by unconscious insect aid; he broadened this by enough detail to warrant the conclusion that in general it serves to ensure cross-pollination by such aid, in this way substantiating Knight's law "nature intended that a sexual intercourse should take place between neighboring plants of the same species"; he gave experimental demonstration of the benefits of crossing, not in itself, but through the interbreeding of individuals which for several generations have been subjected to slightly different conditions, or as he puts it, to "what we call in our ignorance spontaneous variation"; and he showed at once the utility of assured partial self-fertilization as effected by cleistogamic degradation, the benefits of assured crossing resulting from the combined structural and physiological differentiation characteristic of heterogony, and the probability that complete sex-separation "did not commence and was not completed for the sake of the advantages to be gained from cross-fertilization" —but has rather to do with the general problem of division of labor.

His manner of presenting conclusions is at once interesting, convincing and charming. Egotism abounds in his writings; but the "I" and the "my" are not those of the man thinking in first-person pronouns, but of one unwilling to speak in a cathedratic manner and careful to state even obvious conclusions as merely the results to which he as an individual had been unavoidably led. He wrestled with thought synonymy even more earnestly than men now do with that of species; and, for instance, by his use of the word "fertilization," not infrequently compels the reader to take his perfectly unescapable meaning broadly and not too literally; and his inability to find better words to express the significance of floral structures than "adaptation" and "contrivance," reveals the deep basic idea of teleologic causation that the human mind has embodied in the machinery for uttering human thought. His phraseology is often aphoristic. For instance: "No one will understand the final cause of the structure of many flowers without attending to this point" [resultant crossing]; "Who would have been bold enough to surmise that the propagation of a species should have depended on so complex, so apparently artificial, and yet so admirable an arrangement?" [as that in Catasetum]; "A fortunate accident for the plants" [if the detention of moths in securing *Orchis* nectar, long enough for the pollinia to harden on to them were accidental]; "Nature abhors perpetual self-fertilization"; "Belief that flowers of any plant are habitually fertilized in the bud, or are perpetually self-fertilized, is a most effective bar to really understanding their structure''; sexual differences may ''characterize and keep separate the coexisting individuals of the same species in the same manner as they characterize and have kept separate those groups of individuals, produced from common parents during the lapse of ages or in different regions, which we rank and denominate as distinct species''; ''Illegitimate unions [in heterogonous plants] are hybrids formed within the limits of one and the same species.''

Through it all, too, runs a thread of similar sentences revealing the soul of the man, groping only after the truth, to whom ''the whole subject is as yet hidden in darkness.'' In this spirit he lived, worked and wrote. Quite apart from success in accomplishing the direct purpose for which he worked, he succeeded to an exceptional degree in stimulating the research instinct in others, and directing it into attractive and prolific fields, seeing realized almost immediately his prediction that what had been held for trivialities might, when understood, ''exalt the whole vegetable kingdom in most persons' estimation.''

Things did not always go in his work as they were expected to—his first belief that if every bee in Britain were destroyed there would be no more pods on the kidney beans in that country, gave place to the certainty that a small percentage of fruit may set without such aid, and this particular species afterwards gave him less than the customary evidence of the benefits of crossing; but in general his expectation was sustained, or gave place to a better result for his general needs, and incidentally provided a wealth of detail consonant with his evolutionary theories and not yet known to be explicable on other grounds. Aside from this participation in his broader achievements, his work on floral ecology and fertilization, as has been said, has furnished one of the greatest stimuli of modern times to purposeful coordinated observation of minutiæ, not one of which is meaningless—in a field open to all who can see, whether or not enjoying the privileges of great libraries and laboratories.

That he hovered very close to the edge of discoveries that were reserved for others, is clear to every one familiar with his publications. The effect of foreign pollen in modifying the seed (aside from the embryo) and fruit, was early known to him; but neither his studies nor those of others in his day were equal to the demonstration of double fertilization—even as to-day we go no further than the endosperm in accounting for these phenomena. Even his second botanical paper (1858) detailed at length a gardener's observations and his own experiments on a mongrel lot of beans which Darwin had the acuteness to test by growing some of the parent seed as well, and thus to demonstrate that this itself must have been crossed and not pure. Mendel's law—hardly deducible from these facts, but again suggested in his study of the heredity of style- and stamen-length in illegitimate unions of heterogonous species (which he contrasts with hybridization)—escaped him, and the obscurity of its publication seems to have prevented him from enjoying its benefits at all in his analysis of the complex problems of heredity. He was on the verge of knowing the important part that light sometimes plays in the phenomena of germination, but at most barely knew it. To him had not come the fundamental distinction between fluctuating and mutating variations; and the demonstration that cumulation of the latter and not accretion of the former underlies organic evolution was left for others—to whom the basal mystery of causation is likely long to remain as obscure as it confessedly was to Darwin. Convinced, beyond the possibility of doubt, of the benefits of sexual differentiation with attendant union of elements derived from different individuals, he paused before the question why this differentiation is beneficial up to a certain point and injurious if carried still farther; confessing in candor that he did not know what is the nature or degree of the differentiation, and adding with characteristic humility that at the end he still stood in awe before the mystery of life.

Large as is his service to botany, even in the partial field assigned me on this program, it is but an incident in his life-long struggle with this great mystery on the border-line between the discoverable and the eternally unknowable.

### Darwin's Publications on Pollination and Fertilization

1. Bees and fertilisation of kidney beans. Gard. Chron. **1857**: 725.
2. On the agency of bees in the fertilisation of papilionaceous flowers, and on the crossing of kidney beans. Gard. Chron. **1858**: 828–9.—Ann. & Mag. of Nat. Hist. iii. **2**: 459–465.
3. The origin of species by means of natural selection: or the preservation of favored races in the struggle for life. London, 1859, etc. Index.
4. Fertilisation of British orchids by insect agency. Gard. Chron. **1860**: 528.—Entomol. Weekly Intelligencer. **1860**.
5. Fertilisation of Vincas. Gard. Chron. **1861**: 552.
6. Fertilisation of orchids. Gard. Chron. **1861**: 831.
7. Vincas. Gard. Chron. **1861**: 831–2.
8. On the two forms, or dimorphic condition, in the species of *Primula*, and on their remarkable sexual relations. Journ. Linn. Soc., Bot. **6**: 77–96.—Abst. in Gard. Chron. **1861**: 1048–9.
9. On the three remarkable sexual forms of *Catasetum tridentatum*, an orchid in the possession of the Linnean Society. Journ. Linn. Soc., Bot. **6**: 151–7.—Abst. in Gard. Chron. **1862**: 334–5.—Transl. in Ann. des Sci. Nat., Bot. iv. **19**: 204–255.
10. On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. London, 1862, etc.
11. On the existence of two forms, and on their reciprocal sexual relation, in several species of the genus *Linum*. Journ. Linn. Soc., Bot. **7**: 69–83.—Read Feb. 5, 1863.
12. On the sexual relations of the three forms of *Lythrum salicaria*. Journ. Linn. Soc., Bot. **8**: 169–196.—Read June **16**, **1864**.
13. On the character and hybrid-like nature of the offspring from the illegitimate unions of dimorphic and trimorphic plants. Journ. Linn. Soc., Bot. **10**: 393–437.—Read Feb. 20, 1868.
14. On the specific difference between *Primula veris*, Brit. Fl. (var. *officinalis* of Linn.), *P. vulgaris*, Brit. Fl. (var. *acaulis* Linn.), and *P. elatior* Jacq.; and on the hybrid nature of the common oxlip. With supplementary remarks on naturally produced hybrids in the genus *Verbascum*. Journ. Linn. Soc., Bot. **10**: 437–454.—Read Mar. 19, 1868.
15. The variation of animals and plants under domestication. London. 1868, etc. Index.

16. Notes on the fertilization of orchids. Ann. & Mag. of Nat. Hist. iv. 4: 141–159.
17. Fertilisation of *Leschenaultia*. Gard. Chron. Sept. **1871**: 1166.
18. Fertilisation of the Fumariaceæ. Nature **9**: 460.
19. The effects of cross- and self-fertilisation in the vegetable kingdom. London, 1876, etc.
20. The different forms of flowers on plants of the same species. London, 1877, etc.
21. Fertilisation of plants. Gard. Chron. n. s. **7**: 246.
22. Fritz Müller on flowers and insects. Nature **17**: 78.